Geographic Distribution and Regional Impacts of *Oxyops vitiosa* (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), Biological Control Agents of the Invasive Tree *Melaleuca quinquenervia*

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Geographic Distribution and Regional Impacts of *Oxyops vitiosa* (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), Biological Control Agents of the Invasive Tree *Melaleuca quinquenervia*

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ABSTRACT The invasive tree *Melaleuca quinquenervia* (Cav.) Blake is widely distributed throughout peninsular Florida and poses a significant threat to species diversity in the wetland systems of the Everglades. Mitigation of this threat includes the areawide release campaign of the biological control agents *Oxyops vitiosa* Pascoe and *Boreioglycaspis melaleucae* Moore. We summarize the results of this release effort and quantify the resulting geographic distribution of the herbivores as well as their regional impact on the target weed. A combined total of 3.3 million individual *Melaleuca* biological control agents have been redistributed to 407 locations and among 15 Florida counties. Surveys of the invaded area indicate that the geographic distribution of *O. vitiosa* encompasses 71% of the *Melaleuca* infestation. Although released 5 yr later, the distribution of *B. melaleuca* is slightly greater than its predecessor, with a range including 78% of the sampled *Melaleuca* stands. *Melaleuca* stands outside both biological control agents' distributions occurred primarily in the northern extremes of the tree's range. Strong positive association between herbivore species was observed, with the same density of both species occurring in 162 stands and no evidence of interspecific competition. Soil type also influenced the incidence of biological control agents and the distribution of their impacts. The odds of encountering *O. vitiosa* or *B. melaleucae* in cells dominated by sandy soils were 2.2 and 2.9 times more likely than those predominated by organically rich soils. As a result, a greater level of damage from both herbivores was observed for stands growing on sandy versus organic-rich soils.

KEY WORDS herbivory, invasive species, dispersal, weed biological control, postrelease evaluation

Invasion of natural communities by exotic species is a severe threat to ecosystem integrity (Heywood 1989, OTA 1993, Wilcove et al. 1998, Myers and Bazely 2003). Invasive alien plants, for instance, threaten native ecosystems by altering hydrological patterns, disturbance regimens, nutrient cycling, energy budgets, and species diversity (Vitousek et al. 1997, Mack et al. 2000). Tactics for mitigating the spread and negative effects of widely established exotic plants have included mechanical, chemical, and, in some cases, biological control approaches. However, landscape-level control efforts are often limited by the complex matrix of property owners, each with differing priorities and economic resources for the management of invasive plants. In such cases, biological control often represents the only invasive plant management approach that can be uniformly implemented over a large geographic area.

Regional efficacy of biological control is dependent, in part, on the natural enemy's geographic distribution, its population densities, and the suppressive effect per individual (Parker et al. 1999). In early stages of a weed biological control program, the herbivore's geographic distribution is generally limited to initial release localities. However, as host plants deteriorate or individuals enter a dispersive phase, herbivores seek new host patches and the distribution of the nascent population increases across the infested region. The inherent dispersal characteristics of natural enemies are cited as a unique advantage of biological control. Even in programs with rapidly dispersing agents, however, redistribution efforts are often implemented to expedite herbivore spread and impacts. In 1988, a large-scale redistribution effort within the United States was initiated to disseminate nine Eurasian insect species throughout the range of leafy spurge (*Euphorbia esula* L.), resulting in releases of these biological control agents in 188 counties across 19 states (Hansen et al. 1997). Through a similar effort, introduced herbivores of purple loosestrife (*Lythrum salicaria* L.) have been established in 33 states within

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the Unites States and >1500 wetlands across North America (Blossey et al. 2001, Piper et al. 2004). In a successful effort to reverse the socio-economic impacts of water hyacinth invasion on shoreline communities along the banks of Lake Victoria in eastern Africa, several million *Neochetina bruchi* Hustache and *N. eichhorniae* Warner weevils were released in collaboration with the local fishermen of Kenya, Tanzania, and Uganda (Cilliers et al. 2003).

Selection of release points for redistribution programs have been largely based on cooperator availability, local site characteristics, and political pressures (Hansen et al. 1997, Wright 1997). Only recently have predictive models that incorporate weed distribution, agent release points, and herbivore dispersal been used to provide insight to optimal release strategies (Nordblom et al. 2002). A simulation model developed by Pratt et al. (2003), for instance, predicted that dispersal of the biological control agent *Oxyops vitiosa* Pascoe through the range of its host *Melaleuca quinquenervia* (Cav.) Blake (hereafter referred to by the genus) in Florida would require ≈15 yr. However, the model indicated that weevil dispersal to remote *Melaleuca* stands was slow and in a few cases nonexistent. Therefore, an iterative process was used to identify additional release locations, which resulted in the recommendation to release 5,000 weevils at each of 16 additional releases points. This redistribution was predicted to expedite the weevil's spread throughout the tree's adventive range. In response to these results, federal, state, and county agencies initiated a redistribution campaign for *O. vitiosa* and incorporated releases of the second *Melaleuca* biological control agent, *Boreioglycaspis melaleucae* Moore, during 2003 (Center et al. 2006).

Herein we examine the realized geographic distribution of *O. vitiosa* and *B. melaleucae* as a result of this release effort in Florida to test the aforementioned predictions. We also study the landscape-level heterogeneity of herbivore distribution, impacts, and associations among species.

Materials and Methods

Study Species. In its native range, *Melaleuca* occurs along Australia's northeastern coast from Sydney in New South Wales to the tip of Cape York Peninsula in northern Queensland, in New Guinea, and in New Caledonia (Boland et al. 1987). Multiple introductions of *Melaleuca* seeds were made on both the eastern and western coasts of Florida (Dray et al. 2006), resulting in highest concentrations of the weed along the coastal areas south of Lake Okeechobee. The trees, which occur in both dry and flooded habitats, grow at rates of up to 2 m/yr, can reach sexual maturity in <2 yr (Meskimen 1962), and may flower several times per year. The canopy of a mature tree (38 cm diameter at breast height [dbh] and 12 m tall) may hold up to 1.4 kg of seeds (≈56 million seeds, Rayamajhi et al. 2002). Because of the massive seed release from mother trees, dense, monospecific *Melaleuca* stands are common.

A classical weed biological control program targeting *Melaleuca* was initiated in 1986, with expectations that introduced herbivores would limit invasion and compliment conventional control tactics (Balciunas et al. 1994). The curculionid *O. vitiosa* was the first candidate selected for quarantine-based host specificity testing (Purcell and Balciunas 1994) and, once deemed environmentally safe, was released in Florida in 1997 (Center et al. 2000, Pratt et al. 2003). Eggs are deposited on the surface of expanding foliar buds, young leaves, or elongating stems. Larvae are ectophages, feeding on one side of the leaf through to the cuticle on the opposite, producing a window-like feeding scar. After the completion of five instars, larvae drop to the forest floor and pupate in the soil. In the absence of suitable phenological stages of its host, larvae are uncommon during summer months (April to September) unless damage-induced regrowth is present (Center et al. 2000). Adult weevils can live in excess of 1 yr, and females produce ≈350 eggs during their lifetime (Wheeler 2003). Feeding by the weevil markedly reduces the tree's reproductive potential (Pratt et al. 2005), but *O. vitiosa* pupates in the soil so it is unable to thrive in permanently flooded habitats where some *Melaleuca* stands persist.

To enhance landscape-level suppression of *Melaleuca*, a second biological control agent, the psyllid *B. melaleucae*, was released in Florida during the spring of 2002 (Center et al. 2006). By completing its life cycle entirely on the plant, *B. melaleucae* is less vulnerable to hydrological conditions and it exploits a wider range of leaf ages than the weevil (Wineriter et al. 2003). Like all psyllids, *B. melaleucae* passes through five instars, and development from egg to adult spans 28–40 d (Purcell et al. 1997). First instars are active, but later stages are more sessile and congregate on leaves or stems, secreting copious amounts of white, waxy filaments from dorsal glands. Adults and nymphs feed by inserting their stylets through stomatal pores to gain access to the phloem (Purcell et al. 1997, Woodburn and Lewis 1973). Both adults and nymphs feed on expanding buds and leaves, but as competition for these sites increase, nymphs also exploit mature, fully expanded leaves. Initial field data indicate that feeding by psyllids induces leaf senescence, eventually resulting in mortality of coppicing stumps and seedlings (Center et al. 2006, Franks et al. 2006, Morath et al. 2006).

Experimental Design. The distribution of *Melalecua* in Florida was quantified from systematic reconnaissance flights conducted in 2003–2005 by the South Florida Water Management District and U.S. Department of Interior (Laroche 1999, Ferriter et al. 2006). The presence and abundance of *Melaleuca* was recorded from a fixed-wing aircraft at timed intervals along east–west transects that were spaced 4 km apart and ranged from Orlando (28.5° N) to the Florida Keys (24.5° N, Ferriter et al. 2006). The locations of *Melaleuca* trees were acquired with a real-time differential global positioning system affixed to the aircraft. The resulting data were imported into the georeferenced software ArcGis 9.1 (ESRI, Redlands, CA).

Assessing herbivore populations at each *Melaleuca* location was not feasible. Therefore, a two-dimensional matrix of 36 by 50 cells was created. Each cell comprised an area delineated by five longitudinal and five latitudinal minutes, encompassed ≈76 km^2, and had a binary (infested/not infested) representation of the geographical extents of *Melaleuca* in Florida (Fig. 1). For all infested cells, we haphazardly selected a single *Melaleuca* stand from which we assessed herbivore presence, relative densities, and cumulative damage during a 30-min evaluation period. Herbivore density levels by species were categorized as follows: 0 = no herbivores, rare = 1–3 individuals (weevils) or colonies (psyllids) observed during the evaluation period, common = 4–5 individuals or colonies observed on most trees, and abundant = >5 individuals or colonies on all trees. Because feeding damage for *O. vitiosa* is distinctive from that of *B. melaleucae* (Pratt et al. 2003, Morath et al. 2006), cumulative feeding damage for each biological control agent was assessed on a four-point scale based on a visual estimation of the percentage of foliage destroyed by herbivory: 0 = no damage; 1 = <33%; 2 = 33–66%; 3 = >66%.

To elucidate parameters that may influence biological control agent distribution and impact, various characteristics of each sample stand were noted, including distance from nearest release site of the same species, distance from nearest stand harboring the same species, minimum and maximum annual temperature, and soil type. Distances to the center point of release sites and colonies were measured within ArcGis. Daily minimum and maximum temperatures from Florida were obtained from 98 weather stations recorded by the Southeastern Regional Climate Center (NOAA 2007). Mean minimum and maximum daily temperatures were calculated by averaging the daily values across the last 5 yr of observations. Temperature data were gathered from individual weather monitoring stations located <50 km from each study site (Southeast Regional Climate Center 2005). Soils for each cell were classified as either sandy or mucky (peat) soils according to published surveys (Florida Department of Environmental Protection 2003).

Graphical representations of herbivore density and damage across the sampled landscape were developed with ArcGis (Geostatistical Analyst function). Prediction values in unsampled locations were surface interpolated by the Inverse Distance Weighted (IDW) deterministic method using the following criteria: (1) the number of sample points used for interpolation was set to 15, (2) power optimization was used to ensure the weights of each sample point were proportional to the inverse distance, and (3) the search neighborhood shape was circular based on the assumption of no directional influence of measured parameters (Pilkington and Hoddle 2006, Diaz et al. 2008).

Statistics. General linear mixed models were used to examine the influence of independent variables on measured parameters (PROC GLIMMIX; SAS Institute 1999, Littell et al. 2002). Herbivore incidence was analyzed with a binary distribution and logit link function. All other mixed model analyses were conducted with a multinomial distribution and cumulative logit link function. To account for spatial autocorrelation of parameters among experimental units (sampled stands), we used the RESIDUAL keyword in the RANDOM statement. We used the exponential spatial covariance structure, where the covariance between two observations is a function of the distance calculated from the *xy* coordinates. Pearson χ^2 test was used to quantify herbivore association from binary data, and the κ coefficient was used to test the null hypothesis that symmetry of species densities within cells is purely by chance (SAS Institute 1999). All data are presented as means (±SE).

Results

A total of 3,395,294 *Melaleuca* biological control agents have been redistributed to 407 locations and among 15 counties as of May 2008 (Table 1). The number of individuals redistributed varied over time and by species. The period of redistribution for *O. vitiosa* ranged from 1997 through 2003, with the greatest number of insects released in 2001 (>164,000). Redistribution of *B. melaleucae* was initiated in 2002, and annual releases for 2003–2008 exceed 400,000 individuals per year. The spatial orientation of release points suggest that the number of releases per county does not correlate with area infested per county (Table 1). Dade County, for instance, had the highest number of releases (292) yet possessed only 7.8% of the total cells infested by *Melaleuca.* In contrast, Palm Beach County had the greatest area infested by the weed but had received only 7.4% of the total releases.

Systematic reconnaissance flights (SRFs) indicate that *Melaleuca* occurs within 318 of the sample cells and is distributed widely throughout the southern and central portions of the state. We confirmed the tree's occurrence in 223 cells (70%), we were unable to locate the trees in 19 cells after extensive searching, and we were unable to access 76 cells to conduct assessments. However, we found *Melaleuca* in 49 new cells that were not identified during the SRF. Therefore, the number of surveyed cells containing *Melaleuca* totaled 272. Surveys indicated that the geographic distribution of *O. vitiosa* encompasses 200 cells or 74% of cells that contain *Melaleuca.* Although released 5 yr later, the distribution of *B. melaleuca* is slightly greater than its predecessor, with its range including 211 cells or 78% of invaded cells. The cells containing *Melaleuca* yet outside the biological control agent's distribution occurred primarily in the northern extremes of the tree's range in Florida (Fig. 2).

Biological control agent densities varied in space and, to a lesser degree, among species (Fig. 2). Highest densities of both introduced herbivores were observed south of Lake Okeechobee, particularly on the east and west coasts. High *O. vitiosa* densities were observed in 17 cells, medium in 80, and low in 103. Population densities of *B. melaleucae* followed a similar trend with high densities observed in 25 cells,

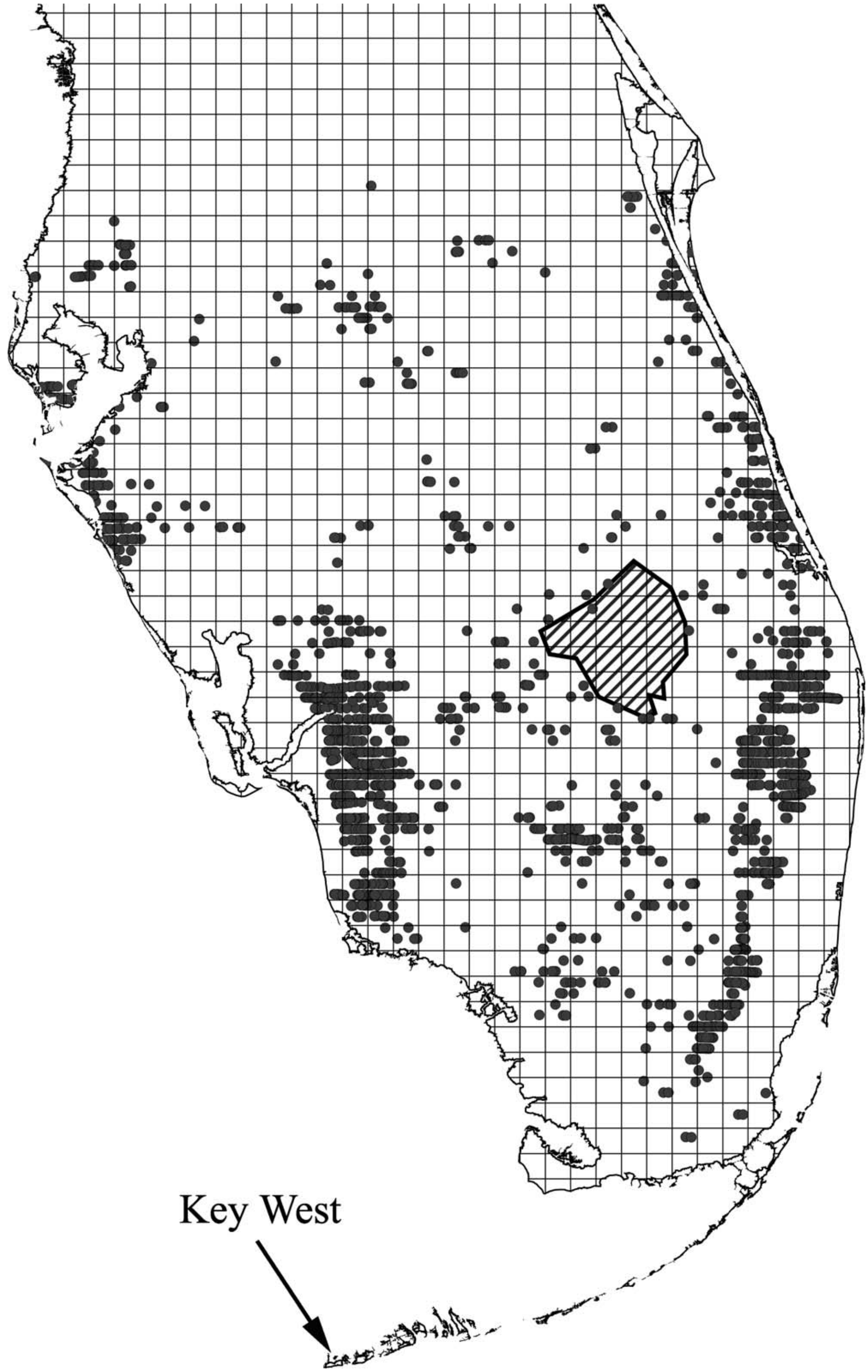

Fig. 1. Geographic range of the invasive tree *M. quinquenervia* for the peninsula of Florida. Dots correspond with observations from systematic reconnaissance flights conducted in 2003–2005. Grid represents sampling cells, which are delineated by 5′ longitudinal and latitudinal lines.

Table 1. Redistribution efforts for the *Melaleuca* weevil (*O. vitiosa*) and psyllid (*B. melaleucae*) in Florida

County	Infested cells[a]	Release dates	Weevil release sites	Individuals released	Release dates	Psyllid release sites	Individuals released
Broward	22	1997–2001	26	16,190	2002–2006	6	241,249
Charlotte	15	1999–2002	1	29,736	2003	1	12,120
Collier	32	1997–1999, 2001–2003	10	83,857	2002–2004	4	141,500
Dade	27	1997–2002	87	224,815	2002–2007	205	1,442,404
Glades	9	1997, 1999–2000	5	5,500	2004	1	13,000
Highlands	10				2004	1	34,000
Hillsborough	9				2004, 2006	2	9,526
Lee	30	1997–1998, 2001–2003	7	95,086	2002–2004	6	63,352
Martin	13	1999, 2001–2002	2	35,939			
Okeechobee	8				2005–2006	1	13,571
Orange	3	2003	1	1,030	2003–2004	2	24,239
Palm Beach	53	1997–2000, 2003	7	14,077	2002–2008	23	1,358,664
Polk	19				2006	1	3,690
Sarasota	18	1999	1	50	2006	1	22,184
St. Lucie	11				2003	2	5,500
Total	279		151	506,280		256	3,395,294

[a] A 5' longitudinal by 5' latitudinal grid was delineated across a map of Florida, and the no. of cells containing *M. quinquenervia* is reported by county.

medium in 86, and low in 100. Strong association between herbivore species was observed in survey cells ($\chi^2_1 = 284.59$, $P < 0.001$). The symmetry in herbivore densities within cells was also high ($\kappa = 0.77$; 95% CI = 0.71–0.82), with the same density of both species observed in 162 cells ($Z = 22.63$; $P = <0.0001$).

There is limited evidence to suggest that maximum temperatures influenced *B. melaleucae* densities and damage (Table 2). Psyllid damage levels, for instance, increased concomitantly with increases in temperature (Table 2). Average minimum and maximum temperatures did not influence weevil incidence, intensity, or impact.

Not surprisingly, herbivore incidence was strongly related to proximity of respective release locations or nearby colonies (Table 2). The odds ratios for both independent variables were negative across species, indicating the probability of occurrence in a given stand decreases with increased distance from populations of the same herbivore species. Soil type also influenced the incidence of biological control agents and the distribution of their impacts (Table 2). From these data, it is estimated that the odds of encountering *O. vitiosa* or *B. melaleucae* in cells dominated by sandy soils are 2.2 and 2.9 times more likely than those with mucky soils, respectively. Herbivory levels ranged widely throughout the state, with highest levels of damage located in the southwestern region (Fig. 2). Statewide herbivory levels were 1.9 ± 0.01 for *O. vitiosa* and 1.7 ± 0.01 for *B. melaleucae.* Foliar damage from both biological control agents was greatest for trees growing on sandy (*O. vitiosa:* 2.0 ± 0.01; *B. melaleucae:* 1.8 ± 0.01) versus mucky soils (1.5 ± 0.2 and 1.3 ± 0.01, respectively). Not surprisingly, herbivore damage was the best predictor of biological control agent densities for both species (*O. vitiosa:* $df_{1,306}$; $F = 1319$; $P < 0.0001$, *B. melaleucae:* $df_{1,359}$; $F = 949.4$; $P < 0.0001$).

Discussion

The objective of weed biological control is to limit the competitiveness of an invasive plant species to facilitate its replacement with more desirable vegetation (McEvoy and Rudd 1993). The realization of this objective has been reported for many biological control programs, but landscape level control is often slow, requiring decades to be realized (Hoffmann 1995, McFadyen 1998). Regional weed suppression may be accelerated, however, through redistribution of natural enemies to remote locations beyond the agent's inherent dispersal abilities. Pratt et al. (2003), for instance, predicted that 182 mo (counting from initial release in 1997) would be required for *O. vitiosa* to disperse from release sites and reach sufficient population densities to cause observable damage to *Melaleuca* trees across 50% of the tree's range. Based on model recommendations, nearly 83,000 individuals were distributed among 16 strategically located release sites in 2002–2003 (Pratt et al. 2003). These additional release efforts were predicted to reduce the time to 50% weevil saturation by nearly 2 yr (a 13% reduction). Our surveys indicate that, 119 mo after establishment, *O. vitiosa* occurs in >71% of the *Melaleuca*-sampled stands at an average herbivory level of two (=33–66% defoliation). Although comparisons between model predictions and realized geographic range are complicated by differing methods of measuring area, these findings suggest that observed dispersal and feeding damage by *O. vitiosa* exceeded model predictions. One explanation for the disparity between observed and predicted herbivore distribution is an underestimation of *Melaleuca* fragmentation in the model, which influences dispersal rates (Pratt et al. 2003). Considering the varying densities of *Melaleuca* in the region, encroaching urbanization, and the patchwork of chemical control efforts, the high rather than the medium fragmentation model may have provided a more accurate representation of the invaded habitat.

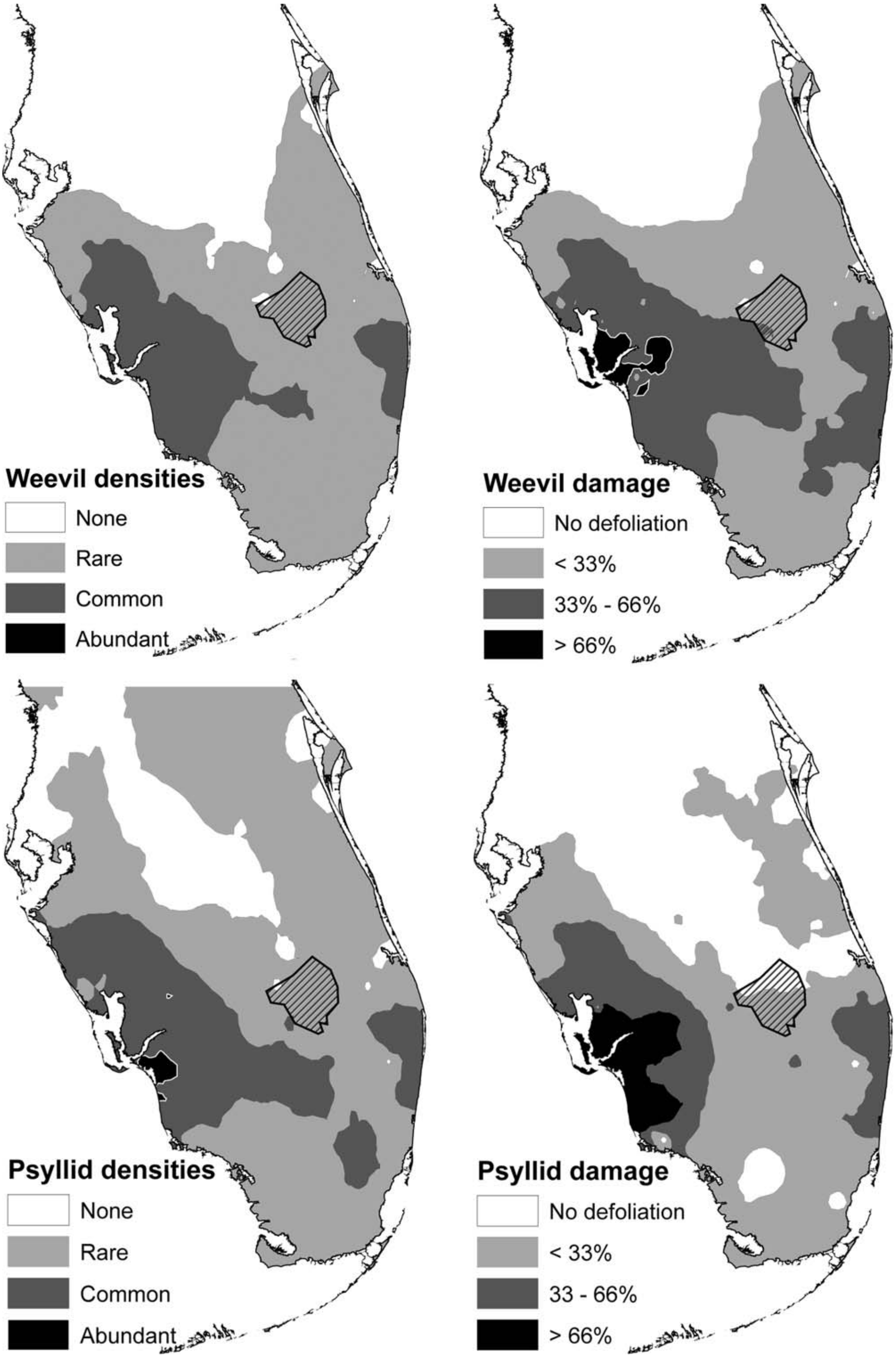

Fig. 2. Geographic distribution, density, and impacts of the *Melaleuca* biological control agents based on a 5′ (=76 km^2) sampling grid. Density levels are presented as follows: 0 = no herbivores, rare = 1–3 individuals observed during 30-min rating period, common = 4–5 individuals observed on many trees, or abundant = >5 individuals on all trees surveyed. Cumulative herbivore damage was assessed on a four-point scale based on a visual estimation of the percentage of foliage destroyed by the natural enemy (see legend).

Table 2. Generalized linear mixed model estimates followed by significance levels (*P*) for the effects of temperature, proximity to release sites or existing colonies, and soil type on the occurrence and impacts of the *Melaleuca* biological control agents *O. vitiosa* and *B. melaleucae*

	Temperature		Release distance	Colony distance	Soil type
	Min.	Max.			
O. vitiosa					
presence	$-0.02; P=0.81$	$-0.23; P=0.43$	$-0.02; P=0.0001$	$-0.07; P<0.0001$	$0.53; P=0.07$
density	$0.04; P=0.26$	$0.12; P=0.28$	$-0.01; P<0.0001$	$-0.01; P<0.0001$	$0.44; P<0.0001$
damage	$0.06; P=0.18$	$0.13; P=0.33$	$-0.01; P<0.0001$	$-0.02; P<0.0001$	$0.54; P<0.0001$
B. melaleucae					
presence	$0.01; P=0.92$	$-0.10; P=0.74$	$-0.02; P<0.0001$	$-0.06; P=0.0008$	$0.70; P=0.017$
density	$0.05; P=0.17$	$0.19; P=0.10$	$-0.01; P<0.0001$	$-0.02; P<0.0001$	$0.50; P<0.0001$
damage	$0.19; P=0.11$	$0.07; P=0.07$	$-0.02; P<0.0001$	$-0.02; P=0.0003$	$0.68; P<0.0001$

Oxyops vitiosa and *B. melaleucae* were released at 151 and 256 *Melaleuca* stands, respectively, which were distributed within 42 and 40 of the delineated cells. The geographic distribution of these herbivores subsequently increased to include 155 new cells for *O. vitiosa* and 171 for *B. melaleucae* (Fig. 2), representing a 3.7- and 4.3-fold increase in range. Dispersal from the nearest release location to the most distant colonized *Melaleuca* stand on the mainland was 93 and 82 km for *O. vitiosa* and *B. melaleuca*, respectively. Based on release dates, the biological control agent's annual rate of spread to these locations was 13.8 km/yr for *O. vitiosa* and 30.9 km/yr for *B. melaleucae*, which are markedly greater than previously reported dispersal estimates (Pratt et al. 2003, Center et al. 2006). The mean spread rate for *O. vitiosa* 2 yr after its introduction into Florida, for instance, was 0.99 ± 0.28 km/yr (range: 0.10–2.78 km/yr) (Pratt et al. 2003). Similarly, *B. melaleucae* spread from release points at a rate of 4.71 ± 0.37 km/yr (range: 2.0–10.2 km/yr). The incongruity between initial rates of spread and those quantified herein may be related to differences in the amount of time used to acquire the estimate. Rates of spread measured over long temporal scales often accelerate with time as founding populations coalesce and competition for limited resources increase (Andow et al. 1993, Shigesada and Kawasaki 1997). Velocity of range expansion for the gypsy moth (*Lymantria dispar* L.), for instance, increased from an initial rate of 9.45 km/yr shortly after the moth's introduction in 1900 to 20.78 km/yr in the 1970–1980s (Liebhold et al. 1992). Similarly, Center et al. (2006) determined that the invasion front for *B. melaleucae* accelerated an average of 225 m/mo. These findings suggest that initial measures of herbivore dispersal provide an essential reference point for examining spread of nascent populations but inferences are limited by the likelihood that spread rates are nonlinear.

Dispersal through diverse plant communities is an important component of herbivore population dynamics and persistence (Jonsen and Roland 2001). The patchwork distribution of *Melaleuca* stands within and between individual cells creates a metapopulation that both facilitates herbivore dispersal and mitigates against local (cell level) extinctions of insect populations. Thus, our data showed that, even though colonies did not persist (i.e., became extinct) at some release points (Center et al. 2000, Pratt et al. 2003), neither herbivore remained extinct in inoculated cells. *O. vitiosa,* for instance, failed to establish when initial releases occurred in permanently flooded habitats (Center et al. 2000). Weevil presence at such sites initially reflected a mainland-island metapopulation model (Harrison and Taylor 1997), wherein laboratory-bred or field-collected *O. vitiosa* were rereleased into those previously inoculated cells that were currently devoid of the insect. Ultimately, however, the spatial variability in hydrological patterns that characterizes southern Florida provided refuges for within-cell persistence in a manner consistent with a patchy metapopulation model (Harrison and Taylor 1997).

The long-range dispersal of *O. vitiosa* to the lower Florida Keys may provide additional insights to the variation in spread rates and dispersal pathways of this species. The distribution of *Melaleuca* in the Florida Keys is restricted to a few ornamentally planted trees on Key Largo as well as a small stand and a few large street trees on Key West. Occurrence of biological control agents on Key Largo is not surprising and most easily explained by natural dispersal from the nearby mainland. However, the presence of *O. vitiosa* on Key West is noteworthy. The lack of *Melaleuca* on the chain of islands between Key Largo and Key West, a distance of >150 km, suggests that winged dispersal is unlikely (Kiritani and Yamamura 2003). It is postulated, however, that hurricanes may facilitate the long-range dispersal of insects (Drake and Farrow 1988), and this line of reasoning may be supported by the five recent hurricanes that bisected Florida in 2004–2005. Another plausible explanation for this and other long distance dispersal events includes human-aided transport, whether unintentional or otherwise. Human activities play an important role in accidental insect invasions, with the most common introduction pathways including transportation of luggage and cargo (Kiritani and Yamamura 2003). Considering the frequent transport of tourists and cargo between the mainland and Key West, the premise that *O. vitiosa* was inadvertently carried or "hitchhiked" to the island remains a plausible explanation. Alternatively, managers of *Melaleuca* infested properties on Key West or other concerned parties may have collected weevils on the mainland and intentionally released them in Key West to facilitate suppression of the exotic tree.

The role of herbivory in regulating plant populations is often influenced by local environmental conditions (Rand 1999). Patterns of herbivory, for instance, may vary according to changes in elevation, temperature, shading, or salinity levels (Lincoln and Mooney 1984, Reynolds and Crossley 1997, Schile and Mopper 2006). Herein, we observed greater levels of herbivory among *Melaleuca* trees growing on arenaceous versus organic soils (Table 2). Soils high in organic matter are often associated with long hydroperiods in southern Florida, and differences in herbivory among soil types may be explained in part by variation in survivorship for soil dwelling *O. vitiosa* pupae. However, *B. melaleucae* is not influenced by hydroperiod and therefore alternative explanations are necessary. Differences, for instance, may also be related to the compensatory abilities of the *Melaleuca* under variable water and nutrient levels (Pratt et al. 2005). Soils high in organic matter have greater water holding capacity and nutrient levels than their sandy counterparts. Therefore, trees growing in organic soils that experience chronic attack from natural enemies may draw on resources more readily to mitigate the effects of herbivory as compared with those under stress in sandy systems. Regardless of the mechanisms involved, it is important to determine if the interaction between herbivory and soil type influences population level changes in reproduction, recruitment, and survivorship of the invasive tree.

Biological control programs often use multiple herbivorous species for the suppression of a common host. These simplified host–herbivore interactions, in the absence of complex trophic relationships, provide unique opportunities to investigate forces that influence community assemblages (Lawton and Strong 1981, Price 1997, McEvoy and Coombs 1999). The role of interspecific competition among phytophagous insects, for instance, has been hotly debated in the scientific literature (Kaplan and Denno 2007), with convincing evidence suggesting that competitive interactions are weak and infrequent among herbivorous arthropods (Lawton and Strong 1981, Strong et al. 1984). Examples from the weed biological control literature, however, indicate that interspecific competition among introduced natural enemies can influence resource availability (McEvoy and Coombs 1999), herbivore establishment (Briese 1997), population growth rates (Woodburn 1996), and geographic distributions (Paynter and Hennecke 2001) of weed biological control agents. Alternatively, species may also act antagonistically through activation of inducible defenses or other mechanisms of interference (Ehler and Hall 1982, Karban et al. 1997). Herein we surveyed *Melaleuca* stands throughout the range of the natural enemies and compared species specific densities for 220 sites. We observed a strong, positive correlation between population sizes of *O. vitiosa* and *B. melaleucae,* indicating that increases in one species does not limit within site abundances of the other. In fact, symmetrical herbivore densities were observed in 162 of the surveyed locations. Consistent with these findings, Franks et al. (2006) investigated the competitive interactions among *O. vitiosa* and *B. melaleucae* when attacking *Melaleuca* seedlings and determined that the effects of the natural enemies were independent. These data indicate that interspecific competition does not currently influence the densities or distributions of *O. vitiosa* and *B. melaleucae.* It should be noted, however, that these herbivores seldom reached population equilibrium as available resources and space were rarely limiting.

In conclusion, we examined the realized geographic distribution of *O. vitiosa* and *B. melaleucae,* two Australian insects introduced into Florida as biological controls of the invasive tree *M. quinquenervia.* Our findings show the insects are distributed throughout >70% of *Melaleuca*'s range in Florida at population levels sufficient to cause substantive damage to the plants. Dispersal rates have increased over initial estimates, in part because of our redistribution efforts, but also as a natural outcome of population growth, coalescence, and metapopulation dynamics. The two species generally co-occurred in *Melaleuca* stands but showed no evidence of antagonistic interactions. Sample cells wherein *O. vitiosa* and *B. melaleucae* remained absent represent small, isolated tree stands or are at the extremes of *Melaleuca*'s range in Florida.

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